Fortschr. Zool. 25, 2/3, pp. 197–221. Gustav Fischer, Stuttgart, New York, 1979.

The Effect of Species of Animals which Share Common Resources on One Another's Distribution and Abundance

L. C. BIRCH

School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia

Summary

The «competitive exclusion» principle has proved to be misleading and too restrictive in the interpretation of how species which share resources influence each other's distribution and abundance. Natural populations do not usually behave as deterministically as deterministic theoretical models and experimental models suppose. In natural populations there is a spectrum of effects of one species on another from nil to complete exclusion. Plenty of species in natural populations share resources and manage to coexist. These cases can be classified into three categories. The density of the species is kept below that at which one affects the other's chance to survive and reproduce. This may be due to the action of any component of environment; predators, pathogens, weather or shortage of resources. Secondly, one species may affect the chance of the other to survive and reproduce but the other has a refuge from which it can recolonize depopulated places. Thirdly, one species may affect the chance of another to survive and reproduce but one is at an advantage at one time and one place and the other at another time or in another place; the advantages and disadvantages balance out. Complete exclusion of one species by another is often inferred from indirect evidence which does not exclude alternative possible hypotheses. Direct evidence for complete exclusion can be obtained by experimental perturbation of natural populations and sometimes by direct observation without perturbation. Direct evidence for complete exclusion is examined in a phylogenetical sequence of examples. In such cases where exclusion has been demonstrated the excluding species makes resources unavailable for the excluded species. This may be through aggression or one species may use up the resource before the other can gain effective access.

1. Introduction

«Looking back» said CHARLES DARWIN, «I think it was more difficult to see what the problems were than to solve them.» Somewhat later GERTRUDE STEIN is reported to have said while dying, «It is better to ask questions than to give answers, even good answers.» It is my purpose to ask questions in an area where many ecologists consider we have good answers. We must question the questions people have asked and see if we can formulate better ones. The trouble about good answers is that people tend to look at problems in terms of answers they already know and which they expect or hope to find.

One of these answers has been the so-called «competitive exclusion principle» or «Gause's rule» which states that two species «competing» for the same limiting resources cannot coexist in the same habitat. Some theories of community structure are based very largely on this principle. For example, WHITAKER and LEVIN (1975, p. 30) wrote, «the combined weight of empirical and theoretical evidence does justify the identification of niche with species within a particular community. This is not a matter of chance, but is the result of competitive exclusion, the dynamic process of natural selection at the species level.» A similar view is expressed by CODY and DIAMOND (1975, p. 8).

For some 20 years or more various criticisms have been made of this «principle» on the grounds of impossibility of proof or disproof, the circularity of the argument and the semantic problems associated with the words «competition» and «same». These criticisms have been made by many authors such for example as ANDREWARTHA and BIRCH (1954, p. 427), COLE (1960), HARDIN (1960), MILLER (1967) and PETERS (1976). The «principle» is now gradually disappearing from the dogmas of ecology. HORN and MAY (1977), for example, tell us that «the principle is not really very helpful» and AYALA (1972) demonstrated that «species competing for limited resources can coexist».

Nevertheless, there are underlying questions to which the «competitive exclusion» principle was the wrong answer. These questions might be formulated as follows. To what extent does one species affect the distribution and abundance of another species when they share resources? How similar in their use of resources may species be and persist together? Or – what relationship, if any, is there between similarity in use of resources and inability to coexist? In my opinion there is considerable merit in avoiding altogether the use of the word «competition» in discussing these and similar questions. Despite efforts to define its use in ecology precisely (e.g. BIRCH, 1957), there is still a diversity of meanings attached to the word. More importantly, no single definition is completely satisfactory and exclusive of effects not meant to be incorporated in the definition.

Figure 1 (from ANDREWARTHA and BIRCH, 1954, p. 427) was based on the results of laboratory experiments. An essential feature of this hypothetical model is that the opportunity for multiplication continues until space or some other resource becomes limiting. The model illustrates the concept that the distribution of species living alone may be broader than its distribution when it shares resources with another species. Species A excludes B from a part of the temperature range B occupies when living without A in its environment. We wrote at the time «the model provides an example of how the component 'other animals' may modify the influence of weather on the distribution and abundance of a species» (p. 427). This is the correct way of looking at this situation, for when one species shares a resource with another species and affects this other's distribution and abundance it does so by modifying a component of environment that acts directly on the other species. It may, for example, modify the availability of space (e.g. for a barnacle to settle and grow) or food.

At the time we published Figure 1 there was no scarcity of laboratory experiments to draw upon to illustrate the principle. Nor was there any shortage of field studies which were being interpreted in terms of such a model. But in very few field studies was there any direct evidence to support this interpretation. In 1954 ANDREWARTHA and BIRCH found

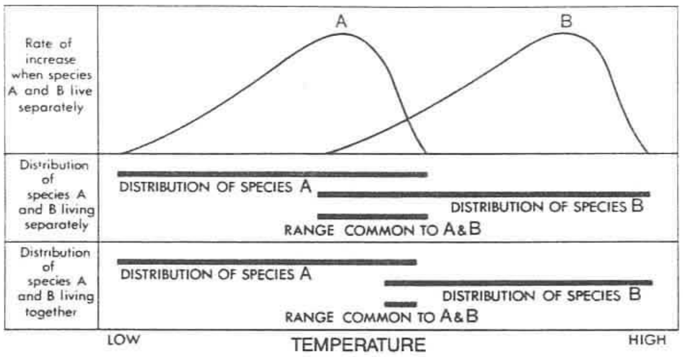
A
B
Rate of increase when species A and B live separately
Distribution of species A and B living separately
DISTRIBUTION OF SPECIES A
DISTRIBUTION OF SPECIES B
RANGE COMMON TO A&B
Distribution of species A and B living together
DISTRIBUTION OF SPECIES A
DISTRIBUTION OF SPECIES B
RANGE COMMON TO A&B
LOW
TEMPERATURE
HIGH

Fig. 1: Hypothetical diagram illustrating one way in which two species which utilize the same resources might reduce the area of each other's distribution with respect to some other component of environment such as temperature.

their best examples from insects in carrion, invertebrates in sewage beds and they quoted one example of inter-species territorial aggression in humming birds by PITELKA (1951). Since then, on the basis largely of theoretical and laboratory models and on indirect evidence such as «character displacement», «niche partitioning», the synchronous disappearance of one species with the appearance of another and on indirect measurements of «competition coefficients» based on habitat overlap, many ecologists tended to accept the model as a principle of nature, as is exemplified for example in the quotations earlier in this paper.

There are all sorts of pitfalls in inferring from these sorts of indirect evidence that one species affects the distribution and abundance of another. HORN and MAY (1977) showed that one method of measuring «limiting similarities» may indeed be measuring something quite unrelated. SCHRODER and ROSENZWEIG (1975) estimated significant «competition coefficients» from habitat overlap of two rodents only to find that perturbation experiments revealed no such «competition» occurring. That one species of animal is observed to increase its numbers as another declines does not necessarily mean that the two phenomena are causally related. For example, the Arctic hare *Lepus arcticus* originally occupied alpine, subalpine and woodland habitats in Newfoundland. Following the introduction of the snowshoe hare *Lepus americanus* about 100 years ago it disappeared from the woodland which was then solely occupied by the snowshoe hare. A popular hypothesis to explain the reduced distribution of the arctic hare is that it was subject to «competitive exclusion» by the snowshoe hare in the woodland. The real story, says GRANT (1972), is probably quite different. The arctic hare is now restricted to places that have ample cover for escape from predators. Furthermore, the principal predator the lynx is known to have increased in numbers following the introduction of the snowshoe hare. The disappearance of the arctic hare from the woodlands could be due to increased predation there by lynx whose numbers increased as a direct result of the availability of snowshoe hare as prey. The arctic hare no longer occupies sections of subalpine and alpine habitats that have poor cover for escape from predators. Nor do snowshoe hares occupy these areas.

CONNELL (1975, p. 461) questioned the assumption underlying the widely held view of community ecologists that «competition is the sole or even principal mechanism determining the area in which one finds a species as opposed to the potential area in which it can live». After reviewing evidence mainly from plants and invertebrates he concluded that «many species seldom reach population densities great enough to compete for resources, because either physical extremes or predation eliminates or suppresses them in the early stages».

There is only one way in which we can know the extent to which species which share resources affect one another's distribution and abundance. The distribution and abundance of the species has to be studied in the field and ideally before and after perturbation of one or other population. Mathematical models and laboratory models are abstractions from reality. To fail to appreciate that is to commit what A. N. WHITEHEAD called «the fallacy of misplaced concreteness». Models have their place in helping us to simplify the complex, but in doing that we need to heed WHITEHEAD's methodological warning «seek simplicity and distrust it».

In natural populations, as distinct from hypothetical ones, exclusion of one species by another is but the extreme case in a gradient of effects that extend from nil to complete exclusion. This we shall see in the examples which follow.

2. The coexistence of species with similar requirements

Many species having similar requirements share habitats and their resources with little or no effect on each other's distribution and abundance. Sometimes it is possible to experimentally analyse the relationships between such species as is illustrated in examples that follow. In other cases this proves difficult to do. For example, VARLEY and GRADWELL (1973, p. 49) state, «In England there are five common species of social wasp of the genus *Vespula* which are all the same size and must compete for food, how they coexist is not fully understood.» FRASER (1976a, 1976b) was unable to find any evidence that two species of salamanders *Plethodon hoffmani* and *P. punctulatus* in eastern North America affected each other in any way despite the fact that they lived in the same places at the same time. The young have very similar diets. The adults differ in size and have some differences in the food they eat. *Plethodon hoffmani* has a contiguous distribution with yet another salamander *P. cinereus*. FRASER (1976b) could find no evidence that they ever ran short of their common food though he thought their nesting sites might be limiting.

2.1. The population density of the species is kept below that at which one can effect the chance of the other to survive and reproduce

Any component of environment may function to keep density low.

2.1.1. Predators

In the lower intertidal zone of the U.S. north-west coast the barnacle *Chthamalus dalli* is unable to survive in the presence of the barnacle *Balanus glandula*. However, in the presence of the snail *Thais*, which preys on *Balanus*, the barnacle *Chthamalus* is able to grow and survive after settling (CONNELL, 1970, 1972). By means of mesh cages CONNELL excluded the predator and was able to show that in the absence of the predator *Balanus* excluded *Chthamalus*.

In the absence of the predatory starfish *Pisaster* the mussel *Mytilus* becomes the dominant species in abundance in parts of the Pacific coast of the U.S.A. In the presence of *Pisaster* the population of the mussel is so reduced that space becomes available for other species to settle. An original eight species increased to 15 (PAINE, 1966, 1974). Even when there is no obviously dominant inhabitant such as *Mytilus* in the sub-tidal zone, the presence of predators may result in increase in the number of species. For example, VIRNSTEIN (1977) studied numbers of species and abundance of bottom macro-invertebrates in caged areas on the sandy bottom of Chesapeake Bay, with and without predators. The main predators were crabs and bottom feeding fish. Without predators he found an average of eight species. With predators the numbers of species increased to 15 after two months. In the presence of predators the abundance of species is presumed to be below the densities at which one influences the chance of another to survive and reproduce and so more species can coexist.

One might anticipate that predators might have a similar effect on terrestrial species though this seems to be difficult to demonstrate. VARLEY and GRADWELL (1973, p. 49) think this may be the case with oak-leaf caterpillars about which they wrote: «There are many species of caterpillars which feed on young oakleaves in spring. They must compete for food at least in those years when the trees are defoliated. We think they coexist because each is regulated by specific parasites at such a low density that collectively they seldom run short of food.»

2.1.2. Weather

Whereas barnacles of the genus *Chthamalus* cannot survive in the lower intertidal zone, in the presence of *Balanus* they do survive in the upper intertidal zone. This is because *Balanus* is unable to survive in the dry conditions there. When DAYTON (1971) arranged streams of sea water above the intertidal zone *Balanus* survived much higher up than usual. Further examples from the intertidal zone of weather reducing the abundance of a species below the density at which it can effect the distribution and abundance of another are given by CONNELL (1975).

Four species of caterpillars feed on the leaves of *Pinus sylvestris* in central Europe. Taking all four species together, outbreaks that result in defoliation of pines and shortage of food have occurred less than ten times in sixty years. The four species, though closely related taxonomically, live on the same trees and so far as can be determined eat the same food which is hardly ever in short supply. It is likely that weather is one of a number of components of environment that keep the populations of caterpillars below outbreak levels most of the time (ANDREWARTHA and BIRCH, 1954, p. 449–9). Without long and detailed studies in the field it is difficult to determine to what extent this phenomenon is common in herbivorous animals.

2.1.3. Shortage of resources

BROADHEAD and WAPSHERE (1966) studied the distribution and abundance of two closely related psocid species *Mesopsocus imminis* and *M. unipunctatus*. They live together in the same trees, feed on the same food *Pleurococcus* and at the same time in larch plantations and mixed woodlands over a wide area of Yorkshire. Individuals of both species occur together on trees and have similar abundance in the same places. Their life histories are very similar. They lay eggs at the same time and the eggs hatch at the same time. They are both hosts to the same two predators. They both increase in numbers together and decrease in numbers together from year to year. They were never observed to run short of food. Only one resource seemed ever to be in short supply. That was suitable twigs on which to oviposit. Only a small proportion of twigs is suitable for oviposition, others being used by other organisms or being in places disturbed by branches or wind. Despite the shortage of suitable oviposition sites one species did not affect the abundance of the other because they had different oviposition preferences. Eggs of the two species were distributed differently along a branch. On thin branches *M. immunis* deposited a greater proportion of its eggs in the axils of the dwarf side shoots than is the case with *M. unipunctatus*. BROADHEAD and WAPSHERE (1966) considered that a shortage of available oviposition sites for both species kept the numbers below the point at which the supply of food became short. There was no indication that one species encroached on the oviposition sites of the other. Had this happenend then doubtless one species would have affected the abundance of the other, depending upon the extent of overlap. BROADHEAD and WAPSHERE (1966) provided data that were convincing to them that the two species of psocids were not kept rare by their two predators. If this is in fact the case then the two psocids are a nice example of two species being kept rare by shortage of resources which they do not share to any significant extent.

In other cases, species that share resources may affect each other deleteriously but not to the extent of excluding each other. This seems to be the case with the two starfishes *Leptasteria hexactus* and *Pisaster ochraceus* in the intertidal regions of the west coast of North America. By means of experimental manipulation MENGE (1972) showed that *Pisaster* inhibited *Leptasterias*. In the absence of *Pisaster, Leptasterias* was larger. In the presence of *Pisaster, Leptasterias* was smaller. Similarly, BRANCH (1976) showed that on a South African shore when barnacle cover increased, the size of the limpet *Patella granularis* decreased. When very abundant, the barnacles completely excluded this limpet.

2.2. One species affects the chance of another to survive and reproduce, but the other has a refuge from which it can recolonize depopulated places

UNDERWOOD (1978) studied the herbivorous gastropods *Nerita atramentosa* and *Cellana tramoserica* which live together on the same rocky surfaces of the intertidal shores of the east coast of Australia. In experimental cages the mortality of *Cellana* was greatly increased with increasing density of *Nerita*. Both feed on microalgae on the surface of the rock. They probably have some feeding differences because the radula of each is different. The densities of animals in the experiments were ones that occur naturally. The inference is that at high densities *Cellana* suffers from having *Nerita* in its environment, probably as a result of a shortage in food induced by *Nerita*. However, both species continue to coexist. Underwood considers this is largely because *Cellana* has subtidal refuges of breeding populations. In addition, *Cellana* has a regular spatial dispersion that probably reduces its pressure on food and, thirdly, there is high variability in space and time in recruitment from planktonic larvae of both species. It is unlikely that high densities of *Nerita* could occur on all shores in every year. When *Cellana*'s population is reduced on any particular shore it can recolonise from elsewhere. A similar situation is described by BRANCH (1976) for barnacles and limpets in South Africa. He found that barnacles crowd out limpets on the rocky surfaces but they continue to coexist. The limpets are replenished by migration and by larval recruitment from sites lower on the shore where there are fewer barnacles.

If carrion alone were the source of food for larvae of the blowfly *Lucilia cuprina* in Australia we might well expect the species to disappear. When eggs of *L. cuprina* are laid on carcases in the field, hardly any survive to become adults. This is almost entirely due to the presence in the carcase of other species especially *Lucilia sericata*. However, the living sheep is a refuge for *L. cuprina*. On the living sheep it is responsible for over 90 per cent of successful «blowfly strikes». There the larvae can develop to maturity in the absence of *L. sericata* (ANDREWARTHA and BIRCH, 1954, p. 449–55).

«Foraging displacement» in birds might be interpreted on similar lines. A bird displaced from an accessible source of food common also to another species will presumably have an alternative though less accessible source of food. MORSE (1967) described the relationship between Brown-Headed Nuthatches *(Sitta pusilla)* and Pine Warblers *(Dendroica pinus)* in long leaf pine forests in Louisiana where they are winter residents. They both participate in flocks of mixed species that form around Chicadees and Tufted Titmice. When alone the Nuthatches forage more heavily on trunks and proximal parts of limbs than they do when with Pine Warblers. When with the Warblers they forage more on the distal parts of lims and on twigs. The Warblers forage on the proximal parts. There were other ways too in which they seemed to divide the habitat between them when together. When together both species are aggressive to each other.

The Plain brown Woodcreeper *Dendrocincla fulginosa* forages close to the ground when following swarms of army ants on Barro Colorado Island in the Panama Canal Zone. In the presence of the Ocellated Antthrush *Phaenostictus mcleannani* they forage on higher or peripheral and less productive areas. They await opportunities to forage in their favoured places if the Antthrush moves away. When the Woodcreeper first occupies a ground foraging site the Antthrush will occasionally dislodge it by snapping at it and fluttering its wings (WILLIS, 1966). It seems reasonable to infer in such cases where one species displaces another in its foraging that the one is having some effect on the other's chance to survive and reproduce, though this might be difficult to measure.

2.3. One species affects the chance of another to survive and reproduce, but one is at an advantage at one time and the other at another time or place. The advantages and disadvantages balance out

UNDERWOOD's (1978) work on the marine gastropods *Nerita* and *Cellana* already referred to showed that *Nerita* had a deleterious effect on *Cellana*. However, it is unlikely that high densities of *Nerita* would occur on all shores of the long coastline in every year. If

Cellana is reduced in numbers, or even becomes extinct, on one shore it can be recolonized from another shore where it is common. This is an additional insurance to *Cellana*'s refuge from *Nerita* lower in the intertidal zone (Section 2.2).

SALE (1978) studied six species of Pomacentrid fish that inhabit together the reef crest and the reef slope of coral reef islands on the Great Barrier Reef. All six species on the reef crest and likewise those on the slope occupy the same space but not at the same time. At any one time individuals of several species will have territories in juxtaposition which they defend against each other and against intruders of any species. But which species occupies a territory seems to be a matter of which arrives first. When a species is removed from its territory its place may be taken by a different species which will then defend the same space against other species including the species that inhabited the space before it. Several species thus coexist, but one affects the distribution and abundance of another at any one time through interspecies territoriality. If one species became much more abundant than the others, this would seem to pose a threat to these others. However, this may be an unlikely occurrence over a large area because of the great diversity and extent of the Barrier Reef.

On the east coast of Australia over a distance of some thousands of kilometres from north to south two species of the tephretid fruit fly of the genus *Dacus, D. tryoni* and *D. neohumeralis* carry out their life-histories in a variety of fruits (LEWONTIN and BIRCH, 1966). Their adults occur together in the same trees, they lay their eggs together into the same fruits in which the larvae develop. The only difference that has been observed is that adults of *D. neohumeralis* are more abundant in trees with lots of shade-giving foliage (GIBBS, 1965). We do not know if the presence of one species in a fruit reduces the amount of food available to the other. The two species of *Dacus* vary greatly in abundance in the same place. Sometimes one is common. At other times the other is common. In another locality at the same time the reverse may be the case. The two species continue to coexist despite their common requirements. It is possible that local populations of one species are made extinct by the other species. Recolonization can then take place from other local populations. This presents no problem at least for *D. tryoni* which we know has a strongly dispersive stage shortly after the adult emerges from the puparium in the soil. FLETCHER (1973) found that 75% of adults that emerged in an orchard left during the first week of life.

3. Exclusion of one species by another

In much of the literature on community structure the distribution of species is interpreted in terms of exclusion of one species by another. It is not possible to know when this is the correct interpretation without direct evidence of exclusion. This may come from direct observation of inter-species antagonism or from observing the effects of perturbation of populations or their resources. Unfortunately, direct evidence has been sought in far fewer cases than those in which exclusion is inferred.

In some cases direct evidence is available that exclusion is happening but not how it is happening. This makes classification of examples difficult. However, in every case where the mechanism is known one species makes resources unavailable to another. This can happen through aggression in which the loser is driven away (some birds) or even killed (some ants) or through more benign interference (limpets and barnacles). Or it may happen when one species uses the resource more efficiently than another so that the other is left deprived (insects in carrion). The resource in all these cases may be food space or nesting sites. Examples are given in the following phylogenetic sequence which method of classification has been followed because the mechanism of exclusion is not known in a number of cases where it can be demonstrated that exclusion occurs.

3.1. Insects

To my knowledge the documented claims for exclusion of one species of insect by another are in the Hymenoptera, with two exceptions, insects in carrion and sewage beds and Tephritid fruit flies in fruit.

Ants

In the west of Scotland *Myrmica rubra* and *M. scabrinodis* sometimes occur together and sometimes separately. In woodland only *rubra* is found; in heath heather and felled woodland both are found, but in the places *M. scabrinodis* lives in short turf and *M. rubra* in longer grass-herb vegetation. This segregation within the heather or felled woodland is evidently not brought about by selection of different places by the ants; it is caused, at least in part, by an active interference of one species by the other (BRIAN, 1956). Colonies are founded in summer. *M. rubra* are the first ants to arrive; their foundress queens form colonies in the warmest places which are wet but not waterlogged. *M. scabrinodis,* which arrives a little later, selects the same sorts of warm and well-drained sites for its colonies. Some or perhaps many of the suitable sites have already been colonized by *M. rubra.* The second arrivals, namely *M. scabrinodis,* lay siege to the nests of *M. rubra,* remove the appendages of the workers and devour their males. This, especially when associated with dry weather, is enough to cause *M. rubra* to evacuate its nests and *M. scabrinodis* takes over the drier parts of areas previously occupied by *M. rubra.* What prevents *M. scabrinodis* from replacing *M. rubra* entirely in this region? The answer to this question appears to lie in a difference of adaptations which gives *M. rubra* an advantage over *M. scabrinodis* in cooler, moister sites of longer vegetation.

Antagonisms of this sort between different species of ants are not particularly uncommon (WILSON, 1971, pp. 447–52). An extreme example is the Argentine ant *Iridomyrmex humilis* which has been successful in a number of places in exterminating native species of ants, as for example in the Mobile area of Alabama (WILSON, 1951) and in Madeira (BRIAN, 1956). Similarly, the introduced fire ant *Solenopsis saevissima* v. *richteri* is antagonistic to native species of ants in the area it has invaded in the state of Alabama, Florida and Mississippi. Since its spread, the native ants *Solenopsis xyloni* and *Solenopsis geminata* and the Florida harvester ant *Pogonomyrmex badius* have become scarce in the invaded area (WILSON, 1951). The ant *Oecophylla longinoda,* native of East Africa, has been destroyed in some coconut plantations by an introduced ant from India, *Anoplolepis longipes* which replaces it in such plantations (WAY, 1953).

BRIAN (1955) studied the foraging habits of four species of ants when a syrup was placed in positions accessible to all four. The syrup tended to become monopolized by one species, usually by that with the nearest nest, though, sometimes by the species which happened to find the syrup first. Occupancy of the food source produced a change in behaviour of the ants; they appeared to be more «possessive» and once the food was being used, other species appeared less willing to trespass.

Bees

The native honey bee of Japan *Apis cerana* is contracting its distribution and being replaced by the introduced European *Apis mellifera* both in apiaries and in mountainous areas where they live wild. *Apis mellifera* monopolises syrup dishes to which both it and *Apis cerana* have been trained to visit. *A. mellifera* is also said to be a more effective fighter and is able to prevent *A. cerana* from stinging it. *A. mellifera* attacks en masse colonies of *A. cerana* which respond by evacuation. *A. cerana* attacks and destroys only weak colonies of *A. mellifera* which do not evacuate their nests when attacked. The spread of *A. mellifera* is aided by man's preference for this bee which he protects in preference to the native one (BRIAN, 1971, p. 92).

In 1957 the African sub-species *Apis mellifera adansonii* was introduced into Brazil. By 1971 it had spread over most of Brazil, Paraguay, Uruguay and parts of Argentina replacing populations of the European bee *Apis mellifera* (MICHENER, 1975). According to MICHENER (1975) and ORLEY R. TAYLOR (personal communication), replacement occurs in two ways; by hybridization and by take-over of colonies. In hybridization «European» characteristics soon disappear. Bees with a predominance of African genes are much «fitter» in the wild in tropical and subtropical areas than the European bees. Occasionally European bees are invaded by «Africanized» bees. Swarms of Africanized bees land on or near colonies of European bees and then enter. The resident queen is killed and «almost overnight the colony is Africanized».

JOHNSON and HUBBELL (1974) found that many species of stingless bees in Costa Rica exhibit both intra-specific and inter-specific aggressive behaviour when they meet on flowers or at artificial baits. The loser in an encounter is forced to spend less time at the food source and gathers less nectar or pollen. At artificial baits the intensity of aggression rose sharply with increased sugar concentrations. Sometimes the aggression is so intense that the loser is killed. In another study JOHNSON and HUBBELL (1975) watched the behaviour of two species of stingless bees *Trigona fuscipennis* and *T. fulviventris* which forage for pollen on *Cassia biflora. T. fuscipennis* forages in groups and tends to restrict its visits to large clumps of *Cassia. T. fulviventris* forages individually and visits more widely spaced or isolated plants of *Cassia*. If *T. fulviventris* happens to visit a clump of *Cassia* it is displaced by the aggressive behaviour of *T. fuscipennis*. This was observed frequently. JOHNSON and HUBBELL (1975) had evidence that the one species had a preference for clumps of plants and the other for isolated plants but that plenty of mistakes were made resulting in aggressive encounters.

Bumble bees

BRIAN (1957) showed that tongue length of four sympatric species of *Bombus* was correlated with depth of flower tube in 15 species of native plant visited by the bees. When given paper flowers (provided with sugar and water) with a range of tube-depth corresponding to the native plants, all species preferred shallow flowers. However, whenever a shorter tongue bee encountered a longer tongue bee it displaced it from the preferred flowers. These aggressive encounters are rarely seen in nature. Brian thought this could be explained in the following way. Her experiments indicated that there was rapid conditioning of individual bumble bees to the colour of flowers. Possibly the bees are rapidly conditioned by aggression to visit only certain flowers. If these interpretations are correct then bumble bees exclude other species of bumble bees from their preferred flowers.

More direct evidence that such is the case in bumble bees is provided by INOUYE (1978). In his study area at Gothic, Colorado, *Bombus appositus* and *B. flavifrons* each concentrated its foraging on a different flower species, apparently choosing the species whose corolla tube length matched its proboscis length most closely. When each bumble bee was temporarily removed from its preferred flower species the remaining bumble bee species increased visitation to the other, previously less utilized, flower species. The remaining bumble bees visited more flowers per stay in the patch, suggesting that they were finding greater amounts of nectar in the absence of the other bumble bee species.

These removal experiments demonstrated that the bumble bees were sampling flowers frequently enough and were flexible enough in their foraging behaviour to respond rapidly to short-term changes in nectar availability. In another area where its preferred flower species and the other bumble bee species were absent, *B. flavifrons* foraged actively on the flower species it rarely used in Gothic. This observation and the experiments demonstrate that resource utilization by a bumble bee species is influenced by the presence of other species.

Hymenopterous «parasites»

DEBACH (1966, p. 200) in his review of the «competitive displacement and coexistence principles» in insects wrote, «Perhaps the only thoroughly documented case of competitive displacement between two ecological homologues involves the closely related species of *Aphytis* in southern California.» Three species of small ectoparasitic chalcid wasps of the genus *Aphytis* complete their life history on the red scale *Aonidiella aurantii*. Each species comes from a different Asian country. Each has virtually identical life cycles. They lay their eggs in the body of the scale beneath the scale covering. Their larvae feed on the scale and pupate there. Adults feed on nectar and honey dew secreted by the scale insects. However, there are considerable differences in their ability to survive and to reproduce at different temperatures and humidities (DE BACH and SUNDBY 1963).

Aphytis chrysomphali was the first to become established about 1900 in the coastal areas of the citrus growing areas of Southern California. Away from the coast in areas «intermediate» between the coastal citrus areas and those in the «interior», the climate appeared to be unfavourable for its increase. It is possible that it may have become established there in low numbers but periodic introductions were necessary to achieve any control of the scale there. This procedure was not an economic proposition in the interior citrus growing areas and so was never tried there (DE BACH and HAGEN, 1964, p. 448).

A second species *Aphytis lingnanensis* colonised the citrus growing areas in 1948–50. It was present then in far fewer groves than *A. chrysomphali*. However, within four years it became the most abundant of the two species in all areas. By 1959 the distribution of *A. chrysomphali* was greatly reduced. It was then restricted to pockets on the coast having practically disappeared in the areas away from the coast.

In 1956 and 1957 a third species *Aphytis melinus* was introduced because *A. linganensis* was not achieving high control in the interior. By 1961 it was well established in the interior but only sparcely on the coast and intermediate areas. At the same time *A. lingnanensis* virtually disappeared from the interior but it persisted in the intermediate and coastal areas.

Table 1 shows that by 1968 *A. chrysomphali* was rare being restricted to a few coastal pockets. *A. linganensis* was dominant in the coastal areas and *A. melinus* in the interior. This was still the case eight years later in 1976 (HUFFAKER and MESSENGER 1976, p. 363).

DE BACH and his colleagues interpret these changes in distribution and abundance of the three species of *Aphytis* in terms of «competitive displacement». What is well documented

Table 1: Percent of five parasites including three species of *Aphytis* in populations of red scale in coastal and interior areas of southern California in 1968. (After DEBACH et al, 1971).

	Coastal areas	Interior areas
Aphytis chrysomphali	0.3	0
Aphytis linganensis	68.2	0
Aphytis melinus	5.7	76.6
Prosaltella perniciosi	25.4	0.1
Comperiella bifasciata	0.4	23.3

is that the distribution of *A. chrysomphali* retracted after *A. linganensis* became established and that the distribution of *A. linganensis* retracted after *A. melinus* became established. When *A. chrysomphali* had the field to itself it was most abundant in the coastal areas and so sparce elsewhere that without repeated introductions it was unable to control its host. Although *A. linganensis* was never alone in the field there is some laboratory evidence that indicates it survives and reproduces better than *A. chrysomphali* in the non-coastal areas. That was where it first became well established. Likewise there was some evidence that *A. melinus* was better adapted to the interior than either of the other two species, which is why it was introduced.

The hypothesis that DE BACH and his colleagues favour is that *A. linganensis* adversely affects the chance of *A. chrysomphali* to survive and reproduce and *A. melinus* adversely affects the chance of *A. linganensis* to survive and reproduce. Although nothing seems to be known about this directly from field studies DE BACH and SUNDBY (1963) did a number of laboratory experiments with *A. linganensis* and *A. melinus* as single and mixed species in population cages at 27 °C. In 8 generations the population consisted completely of *A. linganensis*. The larvae of *A. melinus* had a higher mortality in the presence of *A. linganensis*. The experiments were not done at other temperatures. To obtain direct evidence of this sort from the field it would be necessary to have an area free from *Aphytis*, divide it into plots of single and mixed species all at the one time and follow the fate of all species.

An alternative hypothesis is that the distribution of the three species changed in response to weather during these years. This hypothesis is not excluded by the data although it becomes less likely the longer the present distribution of the three species persists. Any alteration of the present distribution would support this hypothesis.

HASSELL (1976, p. 22) wrote as follows concerning animals in general: «Probably the closest we can get to observing competitive exclusion in operation comes from some examples of species replacement after very similar species have invaded the same area.» He cites as an example three hymenopterous parasites of the oriental fruit fly *Dacus dorsalis*

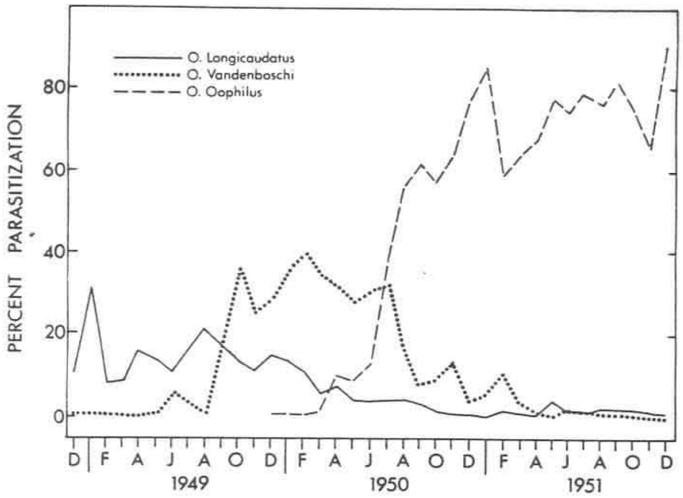

Fig. 2: Changes in the relative abundance of three parasites of the Oriental fruit fly *Dacus dorsalis* on the Hawaiian island of Oahu. (After BESS et al., 1961).

which were introduced into the Hawaiian islands (BESS et al. 1961). Figure 2 shows how *Opius longicaudatus* increased rapidly following its release on the island of Oahu in 1948. Suddenly it declined in numbers in the latter part of 1949. About the same time *Opius vandenboschi,* which had been released about the same time, rose to a peak. However, by 1950 it was on the decline and a third species *Opius oophilus* which had been established in 1949 began a rapid rise in numbers. By late 1951 both *O. longicaudatus* and *O. vandenboschi* had nearly disappeared. According to HUFFAKER and MESSENGER (1976, p. 59) «currently (in 1976) *O. oophilus* is nearly the sole dominant». So the end point of Fig. 1 represents the situation today.

O. oophilus deposits its eggs in the eggs of *Dacus* in fruit. The other two parasites deposit their eggs in larvae. There is some experimental evidence that the presence of an egg of *O. oophilus* inhibits the development of larvae of the other two species (CLAUSEN et al. 1965). Apart from this there is no direct evidence of one species inhibiting another. It is possible that the near disappearance of the two species of *Opius* is caused by the presence of another species. On the other hand it is not unusual in the biological control of insects for a species to multiply for a few generations and then peter out. This is exactly what happened when *Opius concolor* was released in Sicily in an attempt to control *Dacus oleae*. It continued to multiply while releases were being made, that was for several generations. It attained quite a substantial population size, but thereafter when releases ceased its numbers fell and after a couple of years it was very rare (MONASTERO, 1967). In the light of this example it is important to note that the decline of both *O. longicaudatus* and *O. vandenboschi* in Hawaii followed the cessation of releases (Table 2).

On the basis of this information it is reasonable to speculate that *O. longicaudatus* was never going to become established in any case whether or not other species were introduced. The same might be said of *O. vandenboschi* but with less conviction. Furthermore BESS et al. (1961) state that the three parasites have different fruit preferences. Whereas *O. oophilus* was recovered from all fruits, the other two were recovered more frequently from mangos and false kamani than from guavas which are by far the commonest fruit. So by their very habits the two unfavoured species are attracted to less common fruits while the favoured species is attracted to the commonest fruit. Altogether 32 species of parasites have been introduced into Hawaii since 1947 for the control of *Dacus* but only the above three species of *Opius* ever became abundant. Of the remainder, four other species of *Opius* and 3 other genera have been recovered in small numbers (BESS et al., 1961). These, like so many introduced species, just never took on, a fate which probably had nothing to do with the species which did take hold.

Insects in carrion and insects and other invertebrates in sewage beds

Possibly amongst the best documented studies of one species affecting another are on insects in carrion, especially species of blowflies and insects and other animals in sewage beds, which was summarised by ANDREWARTHA and BIRCH (1954, p. 449–55). For example, when eggs of *Lucilia sericata* and *L. cuprina* are laid on carcases in the field hardly any eggs of *L. cuprina* survive to become adults. This is almost entirely due to the presence in the carcase of the other species especially *L. sericata.* (See also section 2.2.)

The Mediterranean fruit fly and the Oriental fruit fly in Hawaii

The Mediterranean fruit fly *Ceratitis capitata* was reported as infesting fruit in the Hawaiian islands early this century. The Oriental fruit fly, *Dacus dorsalis,* was introduced in the 1940's. It spread rapidly. At the same time the distribution of *Ceratitis* has become restricted to higher elevations in peaches and some other fruits and at all elevations in fruits such as coffee that *Dacus* rarely infests.

Table 2: Showing number of *Opius* released in the control of *Dacus dorsalis* on the Hawaiian island of Oahu (after BESS et al., 1961).

Year	Species		
	O. longicaudatus	*O. vandenboschi*	*O. oophilus*
1948	41,772	1,547*	1,547*
1949	78,679	16,643*	16,643*
1950	9,985	8,024	4,257
1951	0	200	937

* The two species were not distinguishable in these two years.

The infestation of both species in guavas in the islands of Lanai in 1950 was studied by KEISER et al. (1974). Figure 3 shows the emergence of flies from guava fruits during the course of six weeks which covers the first crop of guavas. In the first weekly collections *Ceratitis* comprised 66 per cent and *Dacus* 33 per cent of the combined infestation. Thereafter the percentage of *Ceratitis* decreased progressively until at the end of the season the fruit contained only *Dacus*. In the first guava crop the following year *Ceratitis* was again in the fruit before *Dacus* and again by the end of the season none emerged. After some years (which is not stated) DACUS became the sole occupant of guavas.

When both species were allowed to lay eggs into fruit in the laboratory there was high survival of eggs to the adult stage when each species was alone in the fruit. When eggs of both were laid in fruit 99 per cent of the flies that emerged were *Dacus* and only one per cent were *Ceratitis*. It mattered not at all whether *Ceratitis* or *Dacus* laid its eggs first into the fruit. Similarly when eggs were placed by the experimenter in equal numbers in fruit again most of the flies that emerged were *Dacus*. This happened even when the eggs of the two species were placed at opposite ends of the fruit. Whatever the mechanism of suppression is it did not occur in artificial media normally used for rearing laboratory cultures except when the larvae were very crowded.

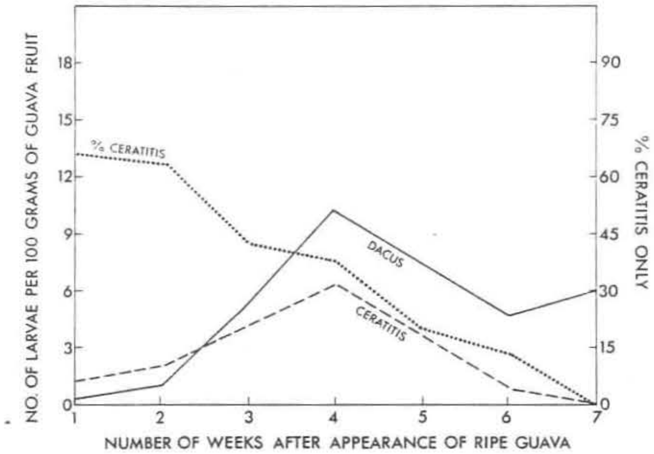

Fig. 3: Changes in the relative abundance of the Mediterranean fruit fly *Ceratitis capitata* and the Oriental fruit fly *Dacus dorsalis* on the Hawaiian island of Lanai in 1950. (After KEISER et al., 1974).

These laboratory experiments together with the history of the two species in the field supports the hypothesis that *Dacus* suppresses *Ceratitis* when they occur together at warm temperatures. At lower temperatures (at higher elevations) *Ceratitis* seems to be the victor. Presumably the process is continuously going on because *Ceratitis* still exists at the lower elevations in coffee and a few fruits that *Dacus* does not use. These are its refuge which possibly prevent complete exclusion.

A similar history of events took place on the east coast of Australia. *Ceratitis* was a major pest of fruit in the fruit growing districts around Sydney sometime during the last century and well into this century. Since about 1945 *Ceratitis* has not been found in Sydney nor anywhere on the east coast of Australia. Its place seems to have been taken by *Dacus tryoni* which is indigenous to tropical Australia further north (BIRCH, 1961). Because *Ceratitis* can no longer be found in Eastern Australia it has not been possible to study the relationship between the two species to see if it compares with studies of *Ceratitis* and *D. dorsalis* in Hawaii. By contrast with this example, *Dacus tryoni* shares fruit with *D. neohumeralis* over a very wide area of Eastern Australia (see Section 2.2).

3.2. Worms

The tapeworm *Hymenolepis diminuta* and the Acanthocephalan *Moniliformis dubius* occur in the intestine of wild rats. Using parasite free laboratory rats as hosts HOLMES (1961) introduced single species and mixed infections with known numbers of parasites. In single species infections the distribution of the two species overlaps almost completely, the tapeworm having the slightly broader distribution. When both species were present there was practically no overlap in the distribution of the two species along the intestine. The effect of the Acanthocephalan on the tapeworm is to reduce its distribution to the posterior part of the length of the intestine it occupies in single species infections. In the presence of the Acanthocephalan the tapeworm was also shorter in length and lower in weight.

In another series of experiments in which the Acanthocephala were newly introduced into rats already infested with tapeworm, the tapeworm became displaced from the anterior region of the intestine. Tapeworms invading established populations of Acanthocephalans caused no change in the distribution of the Acanthocephalan (HOLMES, 1962). Just how the Acanthocephalan adversely affects the tapeworm is not known; HOLMES (1962) suggests that the Acanthocephalan may reduce the availability of carbohydrates for the tapeworm.

REYNOLDSON (1966) investigated the distribution and abundance of four species of triclads that live in freshwater lakes in Britain. All species ate a variety of food, especially oligochaetes and arthropods. But *Polycelis nigra, P. tenuis* and *Dugesia lugubris* preferred oligochaetes whereas *Dendrocoelum lacteum* preferred Crustacea. *D. lugubris* would also eat molluscs but *D. lacteum* would not. The abundance and diversity of food for triclads varied with the concentration of calcium in the water. In lakes with more than 10 mg calcium per litre where food is abundant and diverse the four species were often found living together. *D. lugubris* and *D. lacteum* were not found in lakes with less than 5 mg calcium per litre where food was less diverse and where molluscs and Crustacea had virtually disappeared. REYNOLDSON considered that in these lakes the *Polycelis* species being better adapted to living on the remaining sorts of food, caused a shortage of food for *D. lugubris* and *D. lacteum*. In 41 lakes with less than 5 mg calcium per litre 27 contained *P. nigra* alone, 12 contained *P. tenuis* alone and in two both species were found in the same lake. In only these two lakes was food diverse enough to provide a «food refuge» for the less fortunate species.

The relationship between *P. nigra* and *P. tenuis* was further studied when *P. tenuis* colonised a lake previously occupied by *P. nigra* (REYNOLDSON and BELLAMY, 1970). *P.*

tenuis increased in numbers, the total population of triclads remained about the same and eventually, over a decade, *P. nigra* was reduced to ten per cent of the total. It is possible that *P. nigra* would have declined in any case but this is not likely since *P. nigra* in adjacent lakes did not change in numbers during this same period.

LOCK and REYNOLDSON (1976) provided evidence to suggest that *Polycelis felina* inhibited the growth of populations of *Crenobia alpina* in spring fed streams. Their food requirements are similar. When the food available was increased by artificially removing large numbers of both species the lyo-glycogen food reserves in the animals was increased, suggesting that they had previously suffered from food shortage. Furthermore, a sudden drop in numbers of *P. felina* was followed by a rapid increase in numbers of *C. alpina*. These data are suggestive that *P. felina* inhibited the chance of *C. alpina* to survive and reproduce.

3.3. Marine invertebrates

CONNELL's (1961) experiments with barnacles in an intertidal zone in Scotland demonstrated that the failure of *Chthamalus stellatus* to survive in the lower intertidal zone was due to the presence there of the barnacle *Balanus balinoides*. Figure ~~3~~ shows the results of a typical experiment in which *Chthamalus* had settled in the lower zone and in which *Balanus* were removed as they settled. At the end of a year all the *Chthamalus* that settled in the plot from where *Balanus* were removed survived. None survived in the unmanipulated control where *Balanus* was allowed to settle. In the absence of *Balanus* survival of *Chthamalus* was high in all experiments. In the presence of *Balanus* there was progressive and heavy mortality of *Chthalamus*. *Balanus* makes space unavailable for *Chthalamus* by growing over them, undercutting them and lifting them off the surface or by surrounding them like a tall fence and preventing them from growing. Thus *Balanus* modifies the availability of space which is a direct acting component of environment for *Chthamalus*.

CONNELL (1972) and DAYTON (1971) have shown by means of similar manipulations in the field that on the Pacific northwest coast of the U.S. *Balanus glandula* excludes *Chthamalus dalli* by identical means. By similar means, DAYTON (1971) showed that *Balanus cariosus* excluded *B. glandula* and *C. dalli*. When *B. cariosus* was absent *B. glandula* excluded *C. dalli*.

STIMSON (1970) did a number of experiments which showed that the presence of the limpet *Lottia gigantia* reduced the abundance of other grazing animals on the rocky shore it inhabited on a Californian coast. When *Lottia* found itself touching the grazing limpet

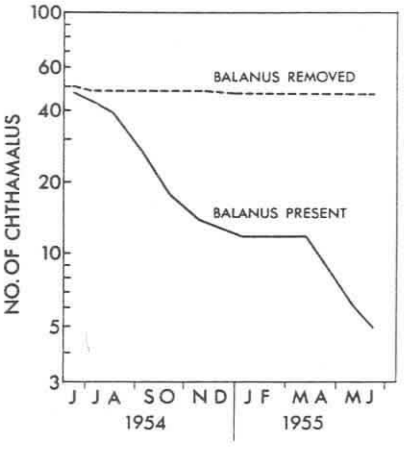

Fig. 4: The effect of removing the barnacle *Balanus balanoides* on the survival of the barnacle *Chthamalus stellatus*. (After CONNELL, 1961).

Acmaea it stopped feeding, retracted its shell, lowered the forward edge then suddenly thrust its shell and moved its foot forward 2 or 3 cm striking and pushing *Acmaea*. Such activities usually displaced *Acmaea* which then got washed away by the next wave. In one such study STIMSON found that the mean number of *Acmaea* in 930 cm^2 quadrats inside the home range of *Lottia* was 4.2 compared with 21 outside the home range. When *Lottia* were removed from areas of rocky shore the number of *Acmaea* increased compared with counts made in home ranges in which *Lottia* were present. Alternatively when *Lottia* were transplanted and established home ranges in a new site the number of *Acmaea* on the site decreased. *Lottia* enters the environment of *Acmaea* as a modifier of space making space unvailable for *Acmaea*. In addition, *Acmaea* can destroy *Lottia*'s food by grazing it down to the substratum. *Lottia* can only feed on a short algal tuft.

A parallel example from the shores of South Africa is provided by *Patella longicosta* which vigorously defends its algal gardens against other limpets (BRANCH, 1975).

When the anemone *Anthopleura elegantissima* completely covers a substratum in the intertidal zone there is no recruitment of barnacles or other rock clinging species. Likewise if barnacles become attached to the surface first they can prevent occupancy by anemones (DAYTON, 1971). In a series of experiments DAYTON (1971) removed barnacles from some areas, keeping others as controls. The immediate effect of removal of barnacles was an increase in the numbers of anemones.

In the intertidal region of Cape Banks near Sydney the limpet *Cellana tramoserica* is abundant in a fairly dry part of the mid-tidal zone. CREESE (1978) found that *Cellana* excludes two other limpets *Siphonaria denticulata* and *S. virgulata* from this area. This happens, not as a result of aggressive activities but because *Cellana* grazes by vigorously scraping the rock surface with a long powerful radula. It is thus able to remove algal spores, diatoms and very small micro-algae from the surface. Because *Cellana* is abundant it is able to prevent any of the algal spores from growing up to form an algal turf. On the other hand, both species of *Siphonaria* have radulae that are adapted to cutting rather than rasping. They are unable to feed effectively on micro-algae. Because *Siphonaria* cannot graze so close to the surface of the rock as *Cellana,* they cannot obtain food from areas where *Cellana* grazes. On occasions when algae do grow to form a turf which *Cellana* cannot graze, *Siphonaria* come in and graze it. But as soon as the algae are closely grazed *Cellana* takes over and crops it to the surface rock. Thereafter as long as *Cellana* is present there is no food for *Siphonaria*, except on the backs of *Cellana* which *Cellana* cannot get at. The three species settle in this area from planktonic larvae and all can live there as tiny limpets when their food requirements are very small. But if *Cellana* is present, before *Siphonaria* is more than a few millimetres in diameter it either dies from starvation or it moves to another zone where algae are more abundant and where *Cellana* does not live.

It does not follow that because the intertidal zone of the shore is a limited space which is well occupied in many places by a variety of plants and animals that one species will necessarily influence the distribution and abundance of another occupying similar space. Sometimes this is so as is indicated in the examples above. More often it is probably not the case (CONNELL, 1975). DAYTON (1973) cleared all organisms from small areas in the intertidal region. He then counted the number of different species recolonizing the area. The number of species increased from zero to six in the first six months, after which the number gradually fell to one species by the 12th month. Did the one surviving species exclude all others by its action either as a direct-acting component of environment of these other species or by modifying direct acting components of these species? DAYTON found that the disappearance of all species except the one survivor was due to a variety of causes. There was always an abundance of unoccupied rock surfaces. Some species of algae died of desiccation, others were grazed off the rocks by limpets and other grazers or were undercut by barnacles. Most of the mussels and barnacles were killed by predators. The only cases in which one species affected the numbers of another as a non-predator entering the environment was the barnacle *Balanus* and the mussel *Mytilus* which smashed or overgrew the barnacle *Chthamalus*.

3.4. Fish

Inter-species territoriality is a means whereby one species may exclude another. Inter-species territoriality has been reported in fish, e.g. GERKING (1959), ISHIGAKI (1966), LOW (1971), THRESHER (1976), EBERSOLE (1977). LOW (1971) found that the pomacentrid reef fish *Pomacentrus flavicauda* responded agonistically to 38 species of 12 families but not to 16 other species of 6 families. *P. flavicauda* defends its home range as a territory. When it was removed from its territory there was increase in other species of algal feeding fish in its former territories. SALE and DYBDAHL (1975) studied 8 species of Pomacentrid fish which held territories throughout their juvenile and adult life. These territories were defended from other species. Their borders were often contiguous and rarely overlapped. SALE (1978) showed that many of these species occupied similar spaces. When he experimentally removed the large species *Eupomacentrus apicalis* from its territories this space was occupied by *Pomacentrus wardi*, a small species, and was held for at least a year against intruding *E. apicalis*. The presence of one species thus excludes another for considerable periods of time.

3.5. Amphibia

Some species of salamanders live close together but in distinctly different habitats. Such is the case with *Plethodon richmondi shenandoah* which is restricted to areas of talus in Shenandoah National Park, Virginia, and *P. cinereus* which inhabits soil outside the talus and does not penetrate into areas of talus, whether or not *P. shenandoah* is present (JAEGER, 1970). From these observations one might infer that the distribution of *P. cinereus* is not influenced by *P. shenandoah*. On the other hand, it is possible that the restriction of *P. shenandoah* to talus is due to the presence of *P. cinereus* in the areas of soil. This is a hypothesis that could indeed be tested. JAEGER (1971) attempted to do just that by enclosing areas on talus and soil. In one lot he placed one species alone, on another the other species alone and in a third lot both species together. He counted survivors after 12 weeks. The idea was sound but unfortunately the design of the manipulations and the small numbers did not permit clear conclusions to be made. They did however suggest that *cinereus* inhibited survival of *shenandoah* in deep soil and also in some other areas.

3.6. Birds

Despite the extent to which the distribution of birds is interpreted in terms of «competitive exclusion» (e.g. CODY, 1974), there is surprisingly little direct evidence of one species excluding another. One sort of direct evidence is inter-species territorial aggression. For example, PITELKA (1951) observed that the male of the humming bird *Calypte anna* was usually successful in preventing the humming bird *Selasphorus sasin* from occupying its territories in Woolsey Canyon in California. From this and other observations PITELKA concluded that the presence of *Calypte* males in the Canyon resulted in there being fewer *Selasphorus* than there would have been if they alone occupied the canyon. Migrant Rufous humming birds *Selasphorus rufus* arrive in eastern Arizona in late summer and there establish feeding territories on their way to their winter quarters in Mexico. They exclude other humming birds from these territories. They are intensively aggressive both to other members of their own species and to other species of humming bird such as *S. platycercus* (KODRIC-BROWN and BROWN, 1978). Further examples of inter-species territoriality in humming birds are given by CODY (1968), STILES and WOLF (1970), FEINSINGER (1976), and LYON (1976).

ORIANS and COLLIER (1963) reported observations which showed that Redwing blackbirds *Agelaius phoeniceus* resident in a marsh prevented the Tricolor blackbird *A. tricolor* from occupying spaces which it would have occupied had the Redwings not been there. Sixteen male Redwings completely occupied the marsh by dividing it up into territories defended by each bird. Tricolor blackbirds made intermittent visits to the marsh but did not take up territories until nine of the Redwings in the centre of the marsh deserted their territories when they were due to breed. Tricolors occupied the centre of the marsh leaving seven territories on the periphery occupied by Redwings. The male Redwings on the periphery of the marsh harassed the Tricolors of both sexes when they returned to the marsh to feed young. They retained their own territories but they did not succeed in establishing any additional territories later in the season.

ORIANS and WILSON (1964) and MURRAY (1971) report further examples of inter-species territoriality in birds and CODY (personal communication) says he now knows of over 60 known species of birds which exhibit inter-species territoriality.

So far as I am aware the only field experiment testing the possible effect of one species of bird on the abundance of another was done by DAVIS (1973). He trapped juncos and golden crowned sparrows for a period of four years in a narrow field, bordered by trees and bushes, about 800 metres long. In this way he established that the juncos were twice as common as sparrows and occurred mostly the whole length of the field in areas with nearby cover close to water. On the other hand, the golden crowned sparrows were concentrated in deep thickets at one end of the field. Juncos fed mostly on seed. The sparrows fed on newly sprouted annuals, buds and flowers. At times they flew together in mixed flocks.

In the fourth year DAVIS removed all 97 of the sparrows he could trap in two months from the whole area. The proportion of juncos in the thicket area of the field rose from 60 per cent to 94 per cent over the next two months. Half the captured sparrows were later returned to the thicket end of the field and the other half further away. About half the latter reached the field in a week. Concurrently, the proportion of juncos in the thickets fell from 94 per cent back to about the proportion they occupied in thickets before the removal of the sparrows. Unfortunately there was no control area. That the junco population rose when the sparrows were removed and fell when sparrows were returned suggests that sparrows excluded juncos from the thickets. As there was no control area other explanations are not excluded.

3.7. Mammals

In western North America several species of chipmunks of the genus *Eutamias* occur on mountains, each species being found at particular altitudes with little or no overlap. Numerous workers have postulated that the zones are maintained by one species excluding the other from areas both might be able to occupy. Numerous studies show that aggressive encounters occur between neighbouring species. Some of these studies have been done in the laboratory, others in the field where the distributions of two species overlap (e.g. BROWN 1971, CRAIG-HELLER 1971, SHEPPARD 1971). However, the critical experimental manipulation of populations involving transplanting populations of one species into the zone of another have not been done, or where tried were inconclusive (e.g. SHEPPARD, 1971). The situation described by BROWN (1971) for the two species *Eutamias dorsalis* and *E. umbris* in the mountains of Nevada invites just such an experiment. On mountain ranges where the two species occur they have different but slightly overlapping altitudinal ranges.

There are two mountain ranges on which only one species occurs. One of these ranges is occupied by *E. dorsalis* alone. The other is occupied by *E. umbris* alone. But each species occupies the total altitudinal range on each mountain. It is of course suggestive that each does this because of the absence of the other species. On the other hand mountains that appear the same to us may not be the same to chipmunks! Until transplantation of populations in such sites are done we shall probably never know the reasons for the different distributions.

Manipulation of field populations has been attempted with mice and voles. Species of *Microtus* are usually found in grassland. Species of *Clethrionomys* are found in woodlands. GRANT (1969) and MORRIS and GRANT (1972) found that on islands where only one genus was present it often occurred in the habitat normally occupied by the other. This suggested that when together one was excluding the other from its preferred habitat. Field experiments show that *Microtus* tended to exclude *Clethrionomys* from grassland when they were both put together in enclosures containing both habitats. When *Clethrionomys* was alone in such an enclosure it occurred more frequently in the grassland than when *Microtus* was also present. Likewise *Clethrionomys* tended to exclude *Microtus* from woodland when both were present in the enclosure with both habitats. Since the information was obtained by trapping it did not provide information on how one excluded the other.

In grasslands inhabited by *Microtus townsendii* the deer mouse *Peromyscus maniculatus* had lower population numbers than when it was alone. To test the hypothesis that *Peromyscus* was driven out of the grasslands by *Microtus*, REDFIELD et al. (1977) removed *Microtus* from two areas (each of 0.64 hectare) where the *Peromyscus* population were «low». One of the areas and its control had only one species of *Microtus* present. The other area and its control had two species of *Microtus*. On the experimental areas *Microtus* were removed every two weeks for three years. On one of the experimental areas, as soon as removal of *Microtus* began *Peromyscus* came in from outside the area and stayed. The original «low» numbers of *Peromyscus* were augmented to 13 after one year and dropped to 6 in the second year. In the control not a single individual of *Peromyscus* was caught. In the second experimental area numbers of *Peromyscus* increased six weeks after removal of *Microtus* began, they rose from one to ten in 12 weeks. A year later there were 26 *Peromyscus*. During this time numbers of *Peromyscus* on the control grid remained between zero and three. *Microtus* were allowed to recolonize the second experimental plot when *Peromyscus* numbers were at their peak of 26 individuals. In ten weeks the numbers of *Peromyscus* declined to six and the numbers of *Microtus* climbed to 70. These experiments demonstrated that in the presence of *Microtus* the distribution and abundance of *Peromyscus* was reduced. The cause was almost complete exclusion by *Microtus* of newly recruited *Peromyscus* and an increase in dispersal or mortality of adult *Peromyscus*. KOPLIN and HOFFMAN (1968) used the removal technique in an attempt to determine if *Microtus pennsylvanicus* excluded *M. montanus* from grasslands. They concluded that it did. However their conclusion has been criticized on the grounds that the size of populations in the controls and the experimental areas were quite different (GRANT, 1972).

In late September 1958 the total population of house mice *Mus musculus* on 22 hectare Brooks Island in San Francisco Bay was estimated to number 12,000 mice. In a little over a year this population had declined to extinction. LIDICKER (1966) studied the population during its decline. The disappearance of the mice was associated with a very short reproductive season, a mere three months, whereas in previous years the population reproduced during most months of the year. LIDICKER was unable to identify any single component of environment that seemed to be responsible for the decline in the *Mus* population. He thought a number of components of environment were involved including the deleterious effect of high populations on the health of the mice, reduced food supply following heavy rains and possible interference by the vole *Microtus californicus*. *Microtus* colonised the island late in 1958 just when the *Mus* population had begun to decline. After an initial slow start it eventually increased its population to 10,000 individuals by the time the last *Mus* had disappeared. It is difficult to believe that *Microtus* was directly responsible alone for the decline of the *Mus* population because *Mus* had declined substantially in numbers well before *Microtus* began to build up. Furthermore, it is well known that *Mus* and *Microtus* exist together in fields on the mainland. On the other hand it is possible that in the population of *Mus* that was declining, for reasons largely unknown, *Microtus* interfered in the nests of *Mus* causing a decline in litter survival that contributed to the eventual demise of the *Mus* population.

There is some evidence that on the mainland although *Mus* and *Microtus* exist together in the same fields *Microtus* reduces the chance of *Mus* to survive and reproduce. An experiment to investigate this was done by DE LONG (1966). He investigated the numbers of house mice *Mus musculus* in field plots in the presence and absence of meadow mice *Microtus californicus*. Two 0.3 hectare areas were enclosed to prevent escape of mice. In one area all field mice were removed. In the other the existing population of field mice and house mice were left intact. Plenty of food was made available to the mice to ensure that there was no food shortage. Each enclosure was trapped every 2 weeks and numbers of mice were estimated by marking, releasing and recapturing.

In the enclosure containing house mice only, their numbers rose to 98 per hectare after 5 months. In the control plots their numbers did not change significantly from a density of about 36 per hectare, however the numbers of field mice trebled. The main difference in the population of house mice in the two enclosures was the number of young entering the population. The reduced recruitment in the mixed population could have been due to direct interference of nests of house mice by field mice which have the habit of entering burrows and disturbing the resident house mice. This could cause desertion of litters or they might even attack and destroy the young house mice. This experiment was deficient in not having replicates and in not having had enclosures in which house mice had been removed. Despite its deficiencies it did however suggest that the field mouse affects the abundance of the house mouse, probably through its direct action in killing the young of the house mouse.

The introduction of sheep, cattle and rabbits into Australia was probably the cause of more extinctions of native mammals than any other causes. This was not because these animals had similar needs to the native mammals. On the contrary their requirements were in many cases very different. The reasons for the extinctions are not known. However as FRITH (1973, p. 109) remarked, «There can be little doubt that alteration of the habitat by stock and the destruction of this cover was the major cause of the decline.» He was referring specifically to the extinction of native mammals in the Riverina district of southern New South Wales. In the mid 19th Century it had a rich marsupial fauna. One expedition recorded 29 species. Today 21 of these species are extinct in the region (FRITH, 1973, p. 108). Except for two small marsupial mice, those that survived were either arboreal, aquatic or like the Echidna and the large kangaroo, extremely adaptable. Stock and rabbits changed the nature of the countryside. The vegetation changed. With overgrazing much of it disappeared altogether leaving denuded plains and sandhills in which native mammals can neither find food nor burrow. Stock made resources unavailable to native mammals by simply destroying the resources. The consequence was that not only herbivorous mammals became extinct but also carnivorous animals such as the marsupial Western native cat *Dasyurus geoffroii*.

Not everywhere in Australia did the introduction of stock mean the decline of marsupials. The reverse is the case with the grey kangaroo *Macropus giganteus* and the red kangaroo *Megaleia rufa* which are both widely distributed in areas occupied by sheep. Both kangaroos probably became more common following the introduction of stock. The causes are not well understood. The presence of sheep means the presence of more watering places and sheep probably changed the nature of the vegetation in favour of the two kangaroos (FRITH, 1973, p. 110).

4. Conclusion

In natural populations of animals that share resources the effect of one species on the distribution and abundance of another varies from nil to complete exclusion. Different species may have very different resource needs and yet coexist in the same place with little or no effect one on the other's distribution and abundance. These examples can be classified under three headings:

1. The density of the species is kept below that at which they affect each other's chance to survive and reproduce. This may be due to any component of environment; predators, pathogens, weather and shortage of resources.
2. One species affects the chance of the other to survive and reproduce but the other has a refuge from which it recolonizes depopulated places.
3. One species affects the chance of another to survive and reproduce but one is at an advantage at one time and the other at another time or place. The advantages and disadvantages balance out.

Complete exclusion of one species by another is more often inferred than demonstrated. Direct evidence requires observation of one species excluding another by aggression or some other activity or observation of effects of manipulation of natural populations or their resources. Without direct evidence it is usually not possible to exclude possible alternative explanations of cases of inferred exclusion.

Where direct evidence is available not only of exclusion but also of the mechanism, one species always excludes another by making resources such as space or food unavailable for the other. This may be through aggression that wards off intruders, or even the killing of the losers or through more benign activities such as a barnacle pushing another off a rock or one species may get access to the resource before the other and uses it up.

Amongst the insects the best documented examples of exclusion of one species by another are in the ants, insects in carrion and tephritid fruit flies. Of two oft-quoted supposed examples from biological control by hymenopterous predators of insect pests, one comes close to making a convincing case of one predator excluding another which time will tell as their histories are followed, the other is more open to alternative explanations. It is quite usual in biological control of insects for many species to be introduced to control a single pest species with successive failures and possibly one or a few species becoming established. Very special evidence is required to attribute the failures to the successful species!

Amongst worms a convincing demonstration of one species reducing the distribution of another is provided by experiments on the effect of a tapeworm on the distribution of an Acanthocephalan worm in the intestine of wild rats (HOLMES, 1961). Here the environment of the parasitic worms (the intestine of the rat in the laboratory) parallels rather closely that of the laboratory models of exclusion of one species by another. In a much less confined environment are the free living planarians in lakes studied by REYNOLDSON (1966) and REYNOLDSON and BELLAMY (1970), who showed that under special circumstances (which limit the common food supply) one species does seem to exclude another.

Amongst intertidal animals the exclusion of the barnacle *Chthamalus* by *Balanus* is well documented by CONNELL (1961, 1972) and DAYTON (1971). The limpet *Lottia* excludes the limpet *Acmaea* on Californian shores (STIMSON, 1970), and the limpet *Cellana* excludes

Siphonaria on Australian shores (CREESE, 1978), and barnacles exclude anemones and vice versa depending on who gets there first (DAYTON, 1971). It does not follow that exclusion is a common determinant of distribution and abundance of intertidal invertebrates, a point of view which has been emphasized in the work of CONNELL (1975) and DAYTON (1973).

Amongst fish, exclusion of one species by another takes place through inter-species territoriality. This appears to be common in some groups such as Pomacentrids. The same is true of birds, with many examples attributed to species of humming birds. There appears to be only one experiment involving field manipulation in birds to test the effect of removal of one species on the distribution and abundance of another species.

In mammals a number of cases of altitudinal distribution of species of chipmunks with little or no overlap provide little convincing evidence for the exclusion of one species by another although this possibility is not excluded. On the other hand, there are convincing experiments in which populations of voles and field mice have been manipulated such that the rise and fall in numbers of one species can be attributed to the fall and rise of the other (GRANT, 1969; MORRIS and GRANT, 1972; REDFIELD et al., 1977; and DE LONG, 1966). Many marsupials in Australia have become extinct, not because sheep, cattle and rabbits that were introduced have particularly similar requirements but because of destruction of cover and other resources by the introduced mammals.

This survey of studies of field populations indicates that conclusions drawn from deterministic theoretical models and laboratory models can be misleading and have led to false generalizations. The models, though logical within themselves, are an abstraction from reality. A stochastic approach which takes into account the patchiness of the environment in space and time, the role of chance events and the spreading of risks within life histories (DEN BOER, 1968) is a more realistic alternative. The modern population biologist needs to heed A. N. WHITEHEAD's warning to «Seek simplicity and distrust it».

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